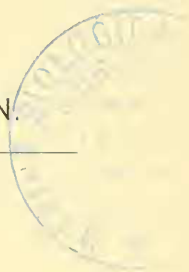


PROCEEDINGS
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BIOLOGICAL SOCIETY OF WASHINGTON.



FURTHER NOTES ON YUCCA INSECTS AND YUCCA
POLLINATION.*

BY C. V. RILEY, PH. D.

PRONUBA MACULATA.

Since the presentation, a year ago, of the communication on "Some Interrelations of Plants and Insects," in which I summarized what was then known of *Yucca* pollination and the *Yucca* moths, some further interesting observations have been made, and the facts which I have to present to-night should be looked upon as additional to those set forth in the previous paper (vol. VII, pp. 81-104). On account of the singular structure of *Yucca whipplei*, which was known to be pollinated by *Pronuba maculata*, I was quite anxious to obtain the facts in reference to this species. The long stamens, the sticky and abundant pollen, and the peltate stigma, with its long hyaline papilla, are characters which would seem to facilitate ordinary pollination, though the restricted style would render this more difficult, and the peculiarities of *Pronuba maculata*, with its modified tongue, and maxillary tentacles very long, and attenuated at tip, were, I felt quite sure, special adaptations to fit it for its work. This *Yucca* is not only one of the most interesting from the structure of its flower, but is one of the noblest of the

* Presented at a meeting of the Biological Society of Washington, May, 1893.

cespitose species and placed in the subgenus *Hesperoyucca*. The flowers are borne in immense panicles on a stalk which arises directly from a crown of leaves near the ground and reaches sometimes a height of twelve feet or more, and I present herewith a photograph which very well illustrates the magnificence of some of the larger specimens (pl. ix). At my request Mr. D. W. Coquillett, of Los Angeles, California, made some special observations last year on the pollination of this species, and on the 12th of June he was able to witness the operations both of oviposition and pollination on a plant while yet the sun was shining brightly, about forty minutes before setting. The act of oviposition does not differ in any particular from that which I have already described in detail for *Pronuba yuccasella*. The pollen is deliberately gathered, and a mass nearly half the size of the insect's head is held under her neck by the coiled tentacles. In pollinating, the tentacles are uncoiled and stretched so that the tips may be inserted into the upper part of the stigma. Mr. Coquillett describes the process of thus pollinating the stigma as lasting about half a minute, after which the insect that he watched descended the ovary and at once mounted to the top of one of the stamens. Here, with her tentacles, she removed both pollen masses (moving her head from side to side during the operation) and added the pollen thus gathered to the mass which she was already carrying. She went to two other stamens in succession, gathering a pollen mass from each. Mr. Coquillett, in communicating his observations, remarks that "it was indeed surprising to witness the evident intelligence which this insect displayed in all her actions wherever the pistil of the flower became pollinated solely through her own labors, and that she went through these maneuvers with the evident intention of pollinating the flower appears to admit of no doubt."

A number of insects have been observed associated with the flowers of *Yucca whipplei*, but none of them as observed by Mr. Coquillett acted in any way to produce pollination, either intentionally or by accident. As a check to prove the influence of *Pronuba* on the production of fruit, I desired Mr. Coquillett to enclose another panicle and exclude the moths. We were both somewhat surprised at the result, namely, that a certain number of the pods set on this panicle, and this would prove that (so far as a single experiment justifies conclusion) the species is capable of a certain amount of self-fertilization.



YUCCA WHIPPLEI.

So far as they go, Mr. Coquillett's observations on the actions of *Pronuba maculata* agree very well with those of Professor William Trelease, who made a special trip through the south-west in the spring of 1892 with a view of studying the pollination of those *Yuccas* which had not hitherto been studied in this connection. He has published a most interesting article in the Fourth Annual Report of the Missouri Botanical Garden, entitled "Further Studies of *Yuccas* and their Pollination." This is, in fact, a most valuable contribution to our knowledge of the subject, and is complementary and additional to my own paper published in the annual report of the same series for the previous year. Mr. Trelease's life studies of *Y. whipplei* have added materially to our understanding of its floral characteristics. The anther cells on dehiscing contract so as to expose the pollen freely, but the contents of each cell forms a "rather consistent, two-lobed moist mass, which is held by its lower part but protrudes prominently from the open anther." The ovary is free from the longitudinal depressions which in the other *Yuccas* usually correspond with the appressed stamens. The capitate stigma is slightly indented at the center "and covered with long, hyaline, delicate papillae which are always moist with abundant secretion that at length becomes almost gelatinous over the middle of the stigma." He found the nectar apparatus well developed, the septal glands, though narrow, reaching commonly to the base of the ovary, with a conducting groove of corresponding size. The glands are, also, though smaller, more active than in most other species of *Yucca* studied by him. Professor Trelease also notes that the characteristics of this flower would seem to make it easily self-fertilizable, and remarks on the exceptional occurrence in the lower part of the Cajon Pass of a few plants with more or less abundant, partly developed, but unusually diminutive capsules, in which no evidences of *Pronuba* action were to be found; and this, added to the experiment made by Mr. Coquillett, would seem to indicate that where *Pronuba* is absent *whipplei* has the same exceptionally limited power of fructification, whether by self-pollination or pollination by other agents, that we know to be possessed by *alaifolia* among the true *Yuccas*. Recognizing this possibility, Professor Trelease was somewhat surprised to find that, with the single exception which he noted, no fruit, among all his observations, was discovered which did not clearly show the work of *Pronuba*.

From his account, as well as that of Mr. Coquillett, it appears evident that *Pronuba maculata*, in accordance with the greater tendency of the flowers of *whipplei* to open during the day, is more diurnal in habit than *Pronuba yuccasella*, carrying on the acts of oviposition and pollination during the day. Further, unlike the other *Pronubas* so far known, this species rests with the head toward the stigma, and when disturbed is very apt to drop suddenly from the flower and take wing. I cannot do better than quote verbatim Mr. Trelease's interesting account of the act of pollination, that of oviposition being, as already stated, absolutely the same as in *yuccasella*:

"Having withdrawn the oviduct, in doing which she moves up so that her head is about level with the stigma, or even before this organ is entirely freed, the moth usually proceeds to pollination; but it is not infrequent for two eggs to be laid between each two visits to the stigma, and, owing to her peculiar alertness, she appears to be even more easily frightened into omitting pollination than are the other species of *Pronuba*. Standing with her head at about the height of the stigma, with the short tongue projecting out in front, she uncoils her long tentacles from the compact mass of pollinia, which she carries similarly to the other *Pronubas*, only that small part of her burden which adheres to the bases of the tentacles being removed from it, and, raising her body on tiptoe, she very slowly saws the tentacles back and forth across the top of the stigma, generally following one of the three shallow grooves, and very carefully working their slender tips into the more or less gummy exudation over the central depression. Sometimes the operation is interrupted long enough to admit of the tentacles being coiled back against the load of pollen and again extended; but the curious manner in which her head is held back from the stigma, as a rule, prevents any of the main load from reaching even the marginal papille.

"On first witnessing this operation I was impressed by the much slower motion of the moth than usual and the evident care which she took to run the ends of the tentacles into the central depression of the stigma, which I then supposed to be solid. The subsequent discovery of the styler canal, communicating with the ovarian cells, showed that it is into this narrow passage that she so carefully guides the tips of her tentacles with their modicum of pollen, and no doubt the abundant stigmatic secretion serves not only to foster the development of the nascent pollen tubes after pollination, but, wetting the tentacles, aids in the disintegration of her mass of pollinia. These, if really related to her work, would seem to have acquired their coherent structure as a means of facilitating their collection rather than as an adaptation to their removal bodily from the anther to the stigma, as is the case in orchids and aselepiads, where, however, special means of secure attachment to the insect accompany this aggregation of the pollen grains into a large mass."

A further interesting fact connected with the pollination of this species is that Professor Trelease discovered a purely black variety (which he describes as *aterrima*) of *Pronuba maculata* connected with the variety *graminifolia* (Wood) of *Yucca whipplei*, common in San Bernardino county. The actions of this black variety are similar to those of the typical form, and it is also diurnal rather than nocturnal in its movements. The method of gathering the pollen mass is thus described:

“Flying into a flower, the moth runs about the bases of the stamens after the manner of other species, then quickly clambers upon the inner side of a filament, and, with the tentacles extended over the pollinia, drags first one and then the other out of the anther cells, pressing them together under the throat, and subsequently compacting the mass together, much as *yuccasella* does the powdery pollen of other *Yuccas*, so that the ball finally consists of as many as ten or a dozen pollinia. So quick and energetic are the motions by which the pollinia are removed that the stamens are often shaken quite violently, as I have before noted in the more nervous attempts of *yuccasella*.”

PRONUBA YUCCASELLA ON THE PACIFIC COAST.

Of the fleshy fruited *Yuccas* Professor Trelease was able to study, among others, *Yucca baccata* Torrey, which is pollinized by *Pronuba yuccasella*. While he was not able to observe the acts of pollination, all the circumstances and the facts which he obtained would indicate that it is precisely the same as described for other species of *Yucca* that are fertilized by this moth, and the fertilized flowers show “conclusively that the pollen is thrust well into the stigmatal canal,” or in some cases apparently even into “the top of the ovarian cells, which, owing to the short style and the deep stigmatic notches, they [the moths] can reach easily with their long maxillary tentacles.” The moths taken from flowers at Cabazon and San Diego are somewhat above the average in size, with the horny and chitinous parts somewhat darker than in the typical form, but specimens which he sent me cannot be considered to have even varietal differences, and find their counterparts in my cabinet in specimens from Dakota and Colorado.

Yucca rupicola Scheele, of southern Texas, and *Y. elata* Engelm., extending from southern Texas to southern Arizona, are both pollinated by *Pronuba yuccasella*, as Professor Trelease ascertained.

PRONUBA SYNTHETICA.

Mr. Trelease was also fortunate enough to be able to study the operations of *Pronuba synthetica* on the flowers of *Yucca brevifolia*. This *Pronuba* is slower in its movements and slower to take flight than the other species observed, though he found it more active during the day than is *Pronuba yuccasella*. It takes wing less readily and then merely sails down to the ground. This indisposition to leave the flower may be connected with the almost constant high winds on the Mojave desert, where this *Yucca* most abounds. The fertilized pistils of this *Yucca* are quite noticeable, by comparison with those of other species, by their symmetry and lack of constriction or indentation so uniformly present in the *Yuccas* that are punctured by *Pronuba yuccasella* and *P. maculata*. The explanation is found in the fact that *Pronuba synthetica* pierces "the uppermost part of the style, conveying its eggs down to the ovary through the stylar channel, the course followed by the pollen tubes." This fact interested me very much, for I recollected very well in my first studies of *Pronuba yuccasella*, before the act of oviposition had been witnessed, that, puncturing for the purpose of oviposition being unrecorded and therefore quite exceptional among Lepidoptera, I was strongly of the opinion that the egg would be thrust through the stigmatic opening down the stylar channel. The instinct to oviposit only on the youngest flowers is particularly marked in *synthetica*, which Trelease frequently saw forcing itself into the narrow clefts between the rigid sepals of the opening bud, the flattened form of the insect facilitating the operation. This habit also suggests the cause of the looseness of the wing scales and the ease with which they are lost. Mr. Trelease's observations in detail on the actions of this *Pronuba* cannot well be condensed, and I quote them entire:

"When about to deposit an egg, having selected a suitable flower, the female of *synthetica* runs to the bottom of the stamens much as *yuccasella* does, makes a rapid, more or less complete circuit of their bases, and then quickly ascends to the very top of the pistil, her thorax rather higher than the end of the stigma, and with her short but strong ovipositor cuts through the thin wall, into the stylar channel, rarely as much as 2 mm. below the tip of the stigma, meantime holding fast to the pistil, the stamens being below her reach. The long extensile oviduct is then passed through the puncture, the egg being laid apparently within the ovarian cell, along the funicular end of the ovules. In removing the oviduct the

moth not infrequently carries her body across the stigma, so that at first sight she appears to be withdrawing it directly from the mouth of the stylar canal; but I have never seen her make direct use of this canal. The operation consumes more time than does the oviposition of either *yuccasella* or *maculata* as I have observed them, and usually takes altogether from two and a half to three minutes. Sometimes two or more eggs are laid before the stigma is pollinated, but commonly after laying each egg the moth retreats to the bottom of the flower and then again ascends the pistil until her head is brought even with the stigma, when she uncoils the large tentacles from their resting-place against her load of pollen and passes them back and forth in the stigmatic chamber, with almost the same motion as the eastern species, usually making use of one of the stigmatic notches. While so employed she carries the rather short tongue almost straight out above the stigma, but I have never seen her make any use of it to force pollen into the latter, nor has she been observed to attempt to feed on the slight stigmatic secretion, nor to search for food at the base of the flower, where, if anywhere, the nectar of the septal glands should be found."

Professor Trelease has not yet published anything upon the other species of *Yucca* insects which he collected, and I take this occasion to present some few unrecorded facts in reference to some of the species of *Prodoxus* which he was kind enough to send me, as also some additional data from other sources.

THE SPECIES OF *PRODOXUS*.

Prodoxus coloradensis.—This was described by me from a single male taken in 1884 by Mr. H. K. Morrison in Colorado. In April, 1892, Mr. F. V. Coville, the present botanist of the Department of Agriculture, gave me a few small pieces of the flower-stem of a *Yucca* infested by a *Prodoxus* larva. The plant was collected in the Charleston mountains, Lincoln county, Nevada, the previous February, and was undoubtedly *Yucca baccata*. From these pieces of stem I reared early in the present month two imagos which proved to be *Prodoxus coloradensis*.

I have also received from Professor Trelease four other collected specimens, rather battered and imperfect, which belong to this species, all taken from the flowers of *Yucca baccata* at Banning, California. These two bred specimens are constant and agree thoroughly well with the type, except that there is no inclination to pale yellowish in the white scales of the head, and the thorax shows some black scales on the tegulae, a line of black around the collar, and, in one of the specimens, along the

middle of the thorax; characters not noticeable except in well-preserved specimens. The white portion of the antennæ extends also in these two specimens beyond the basal third and fully to one-half the length of the organ. The four collected specimens from Professor Trelease indicate considerable variation; in one specimen the outer arm of the transverse Y-band across the posterior portion of the wing being absent, while in another it is broken, as is also the basal portion of the median band. The same is true of the band across the middle of the wing, while the upper portion of this band is connected with the basal band. The larva shows no striking characteristics, but is very similar to most other *Prodoxus* larvæ, being uniformly yellowish-white, the head and cervical shield anteriorly slightly darker, the ocelli black, and the mandibles brown and three-toothed.

Prodoxus reticulatus.—One of the specimens received from Trelease taken in flowers of *Yucca whipplei*, variety *graminifolia*, at Arrowhead Springs, in California, would indicate that this species, which I described from three females from Los Angeles county, California, and the habits of which were not known, breeds in some part of this *Yucca*. The single female sent by Trelease is interesting in that it shows some variation in the direction of *coloradensis*, especially by the separation of the basal half of the W-shaped band.

Prodoxus cinereus.—A section of the flower-stem of *Yucca whipplei* sent me by Mr. Coquillett last July contained a number of different larvæ, and among them most numerous one which subsequently proved to be the larva of *Prodoxus cinereus*. We have known that this species breeds in the main stem of this *Yucca*, but none of the early states had been observed. The larva is remarkable in that it differs materially from the typical *Prodoxus* larva. It is, first of all, very much more elongate, with the sutures between the segments more strongly impressed. It is, farther, more uniform in diameter than the typical *Prodoxus* larva; but the most striking feature is the anal segment, which bears on its ventral plate two stout, brown, decurved horns resembling those of the larva of *Trogosita* in Coleoptera, except that these are curved in the opposite direction. I add a technical description:

PRODOXUS CINEREUS. *Larva*.—Average length when full grown, 8.25 mm.; body elongate, but slightly curved, the joints moniliform; head rather large, more horizontal, and more free than in other species, light brown in

color, darker anteriorly; borders of clypeus almost white; pigment spot around ocelli, and the mandibles dark brown; the Y-shaped lines distinct and having exactly the outline of a rather narrow wine glass; cervical shield pale, but fuscous around the borders and especially at the middle of the anterior border; sinuate laterally and cleft posteriorly by the pale mesial line; characteristic feature a pair of decurved, dark, horny anal hooks, situated on the ventral apex; anal plate but faintly chitinous and with a fuscous mark upon it; a sub-ventral depressed line but faintly indicated and more highly polished than the rest of the surface; spiracles extremely small, with a faint yellow annulus, the prothoracic pair situated on the sub-ventral depressed line, the others much higher up on the anterior third of the segments; no thoracic legs, but slight tubercles in place of them; general color faint bluish-green or yellowish-green, losing color, however, in alcohol.

Pupa.—Offering no peculiar structures, but presenting the characteristics of the other species of the genus; skin very delicate; the cephalic projection not very prominent and the anal tip absolutely smooth; dorsal spinules reduced almost to obsolescence. The shrunken larva skin with its two strong hooks remains attached to the tip of the body of the pupa, and doubtless serves to hold it secure when it pushes from the surface of the thin epidermis to give forth the imago.

The imagos issued from the 11th of April to the 8th of May, the antennal sheaths and leg sheaths of the pupa separating, the former curling very much, as in other Lepidopterous pupæ which have wood- or pith-boring larvæ.

Prodoxus venescens.—Professor Trelease has sent me a full account of the oviposition of this species upon *Yucca whipplei*, and it corresponds in every particular with the oviposition of *Prodoxus decipiens* in the East. In this case the species is not confined to one or the other of the forms of *whipplei*, but occurs on both the typical form and the variety *grammifolia*.

Prodoxus intermedius.—This species was described from two female specimens taken in Texas and one taken in Colorado, in 1887. It is a most interesting form, bearing an even more deceptive resemblance to *Pronuba yuccasella* than does the much commoner *Prodoxus decipiens*. For though the female lacks the remarkable maxillary tentacles of *Pronuba*, the ovipositor is long and delicate, very much as in the latter species. I have been anxious, since publishing the original description, to obtain a male of this rather puzzling species, and, fortunately, Professor Trelease sent me specimens associated with the females. On a superficial examination the males of this species would be separated with great difficulty from the males of *Pronuba yuccasella*; but upon denuding the genitalia the differences at once appear,

and it is curious to note that while the form of the genitalia, though showing slight variation, corresponds with that of *Prodoxus decipiens*, yet the claspers agree more nearly with those of *Pronuba yuccasella*, in having but the one large tubercle.

Prodoxus intricatus sp. nov.—I recently received from Mr. J. T. Mason, who has been kind enough to observe and collect some of the *Yucca* insects for me, a number of specimens of a *Prodoxus* which he found in the flowers of one of the tree *Yuccas* in Jalapa, Mexico. He sent also flowers and sections of one of the leaves of the *Yucca*, which, from this material, appears to be, without much doubt, *Yucca guatemalensis*. The moths were found abundantly in the flowers, but unfortunately reached me in rather dilapidated condition. The species is of the same general size as *Prodoxus reticulatus*, and with a somewhat similar but more varied and less distinct maculation. It is, however, a much darker species. I would simply characterize the species here, by comparison with *reticulatus*, with a view of adding one more link in our knowledge of the *Prodoxids* associated with the different species of *Yucca*.

In size and general appearance most nearly related to *P. reticulatus*, the general color, however, more sordid, the lighter shades inclining to pale fulvous, with a slightly golden sheen. Primaries more acuminate at apex, and marked with black scales, taking on, in a very general and indefinite way, the pattern of those of *reticulatus*. Secondaries also more acuminate at tip and blacker. Fringes of all wings black. Under surfaces fuliginous, with the faintest trace of pale marks on the costa of primaries. Anal claspers of male short, recurved upward, with a rather angular production on the inferior margin, and with three minute, but distinct, black teeth. There is also a similar black tooth on the inner margin near the tip. Ovipositor of female similar to that of *reticulatus*.

Some of the darker specimens present an almost black appearance, the black marks inclosing narrowed, luteous spaces, which appear like so many spots.

Described from 20 males and 5 females, none of them in perfect condition.

CONCLUSIONS.

The additional facts which I have thus presented upon this subject of *Yucca* insects and *Yucca* pollination serve to confirm the generalizations which I have already indulged in. So far as variation is concerned they add still further links to the chain of alliances between the different forms of this interesting family,

Prodoxida. The black form of *Pronuba maculata* presents us with the question of varietal or specific value that has arisen with the plant itself upon which it occurs, so far as regards the variety *graminifolia* of *Yucca whipplei*. Most specialists would be inclined, without any intermediate specimens, to characterize this black form as a distinct species, especially as it is dissociated from the other more typical forms and confined to one particular variety of *Yucca*. Yet in every other character but color it agrees precisely with the typical *maculata*, and I am strengthened in my view of considering it a mere variety by the well-known variation in the maculation of the typical species. It is a form that is differentiated as to color without having yet acquired any essential structural differences, though it may have lost the power to intercross with the typical form. Here, also, the color must be looked upon as of secondary importance to the species, and more or less fortuitous, as it is difficult to see what advantage the purely black has over the maculate form, especially in an insect essentially diurnal.

So it is in the variation of the banded species of *Prodoxus*. Some of the specimens combine the characters of at least two different species, without being referable to either, satisfactorily, and in the present state of our knowledge most entomologists would be justified in describing them as distinct species; but there can be little doubt that, when abundant material from different localities is obtained, all these transversely-marked forms will be difficult to separate. Such, however, is the case in almost every genus, whether of plants or animals, and the Prodoxids simply furnish us with a rather marked illustration of the fact that the variation has gone on and is going on, so far as purely colorational characters are concerned, without any very definite and unchangeable differences having yet been acquired. How strikingly such facts compare with the permanency, even in colorational characters, of such well-established species in the same order as the cosmopolitan *Vanessa cardui*, which, with a most beautiful wing design and a most complex colorational pattern on the inferior surfaces, remains essentially constant in all its details in all parts of the world where it is known.

The decurved hooks in the larva of *Prodoxus cinereus* are also most interesting from an evolutionary point of view. Such anal hooks are extremely rare in Lepidopterous larvæ, being found in